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TETHERED FLIGHT CHARACTERISTICS OF MALE AND FEMALE PEAR PSYLLA (HOMOPTERA: PSYLLIDAE): COMPARISON OF PRE-REPRODUCTIVE AND REPRODUCTIVE INSECTS

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Abstract.—In tethered flight experiments, female winterform pear psylla (*Cacopsylla pyricola* Foerster) exhibited longer mean flight durations and a higher frequency of long duration flights (> 15 min) than did males. Pre-reproductive psylla (collected from the field in mid-winter) exhibited longer duration flights than did psylla collected from the same orchard after egg-laying had commenced. Flight durations decreased with consecutive flights. Although tibia length and wing size were larger for females than males, there was no evidence within sexes or collection dates that body size and flight duration were correlated.

Key Words.—Insecta, tethered flight, pear psylla, body size

Pear psylla, *Cacopsylla pyricola* Foerster, is a specialist pest of pears in many pear growing regions of the world. The species is seasonally dimorphic (Oldfield 1970). The overwintering generation (winterform) undergoes a reproductive diapause in the fall, characterized by a lack of mating and immature ovaries (Krysan & Higbee 1990), and (for a large fraction of the population) dispersal from pear orchards (Horton et al. 1992). Reentry into pear orchards, ovarian development, and egg-laying occur in early spring as temperatures rise (Krysan & Higbee 1990, Horton et al. 1992).

For many insect species, diapause, reproductive status, and dispersal are closely linked life history components (Johnson 1969). Earlier work failed to demonstrate large differences between tethered flight activity of diapausing and post-diapause (but pre-reproductive) female winterforms (Horton, unpublished data). This study compared flight characteristics of psylla collected from the field in mid-winter (pre-reproductive) with those of psylla collected from the same orchard once egg-laying had commenced. We also compared flight characteristics of males and females for both pre-reproductive and reproductive psylla. In several other insect species, females appear to be the more dispersive sex (Adesiyun & Southwood 1979, Reader & Southwood 1984, Davis 1986). Finally, we recorded several wing- and body-size measurements to determine whether flight capacity was related to body size.

Materials and Methods

Flight Methods.—Winterform pear psylla were collected from a commercial pear orchard in Yakima, Washington on two occasions: 19–22 Jan 1993 and 29–31 Mar 1993. Egg-laying had commenced in the field by the March collection; dissections indicated that psylla collected in mid- to late-January had immature ovaries (first mature eggs in dissections were not noted until the first week of March: DRH, unpublished data). Psylla were separated by sex and placed in 150

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ml screened vials (5 per vial) on field-collected pear shoots. Vials and psylla were placed in the flight room (25° C; 85% RH; 10:14 h [L:D]) for 24 h; psylla were flown in the morning (0900 PST) and afternoon (1300 PST) of the day following collection.

The tip of a nylon brush bristle (5–8 mm in length) was attached to the mesothorax of psylla using a small drop of a cyanoacrylate glue (INSTA-CURE®, Bob Smith Industries, Atascadero, CA). The other end of the bristle was attached to an insect pin, which in turn was stuck in a styrofoam block. Psylla were immobilized for gluing by lightly etherizing them. After being glued, psylla were placed in a cold room (3° C) for 30 min to recover from handling.

The flight chamber was a 0.5 m × 0.5 m × 0.5 m box with white sides, a plexiglass top, and an open front. The chamber was illuminated by two 20 watt cool white fluorescent bulbs that were suspended 1 m over the box. Flight durations were timed with the aid of a personal computer and BASIC program. Upon removal from the cold room, psylla were allowed a 15 min "warm-up" period before initiation of the experiment. If flight was not initiated voluntarily, we lightly blew a puff of air at the posterior end of the psylla. Each psylla was flown 5 times, with a 5 min rest period between consecutive flights. Exceptions were psylla that flew continuously for at least an hour; for these psylla, the experiment was ended at 1 h. Sample sizes were 32 to 39 psylla for each sex × collection date combination.

Body Size Measurements.—Following the flight experiments, body size measurements were made using a dissecting scope and ocular micrometer. Measurements were made of tibia length and four wing characteristics. For tibia length, a hind leg was cut off at mid-femur and laid flat on the platform, with the outward portion of the leg facing up. The tibia was measured from the posterior distal point to the knob at the anterior proximal end. For wing size, a forewing was cut off near the base, laid convex side up, and then covered with a glass cover slip. Wing measurements included the distances between the following: (1) fork of the median (M) and cubitus (Cu) veins to the fork of Cu_{1a} and Cu_{1b} veins (measure LRC in Nguyen 1985); (2) fork of the Cu_{1a} and Cu_{1b} veins to the fork of the M_{1+2} and M_{3+4} veins (measure LCM in Nguyen 1985); (3) fork of the M and Cu veins to the apex of the wing; (4) termination of the Cu_{1b} vein to the costal vein break. The latter two estimates were included to provide some indication of overall wing length and width, respectively.

Data Analysis.—For each insect, three measures of flight duration were monitored: duration of the longest flight, mean flight duration (of consecutive flights [up to 5 flights per insect]), and duration of the first flight. Flights of 60+ min were scored as 60 min. These data were analyzed with two-way (sex × reproductive status) analysis of variance (ANOVA). We caution here that the data departed significantly from the assumption of normality (even if transformed), results not uncommon in studies of tethered flight (Davis 1980). Because ANOVA assumptions were not met, marginally significant results should be accepted only cautiously. For insects that completed 5 flights, we included flight number (first through fifth) as a factor in a repeated measures ANOVA; this analysis allowed us to determine whether flight duration changed between one flight and a subsequent flight. Body size measurements were compared between sexes and collection dates using multivariate analysis of variance (MANOVA). All analyses were done in the PROC GLM package of SAS (SAS Institute 1987).

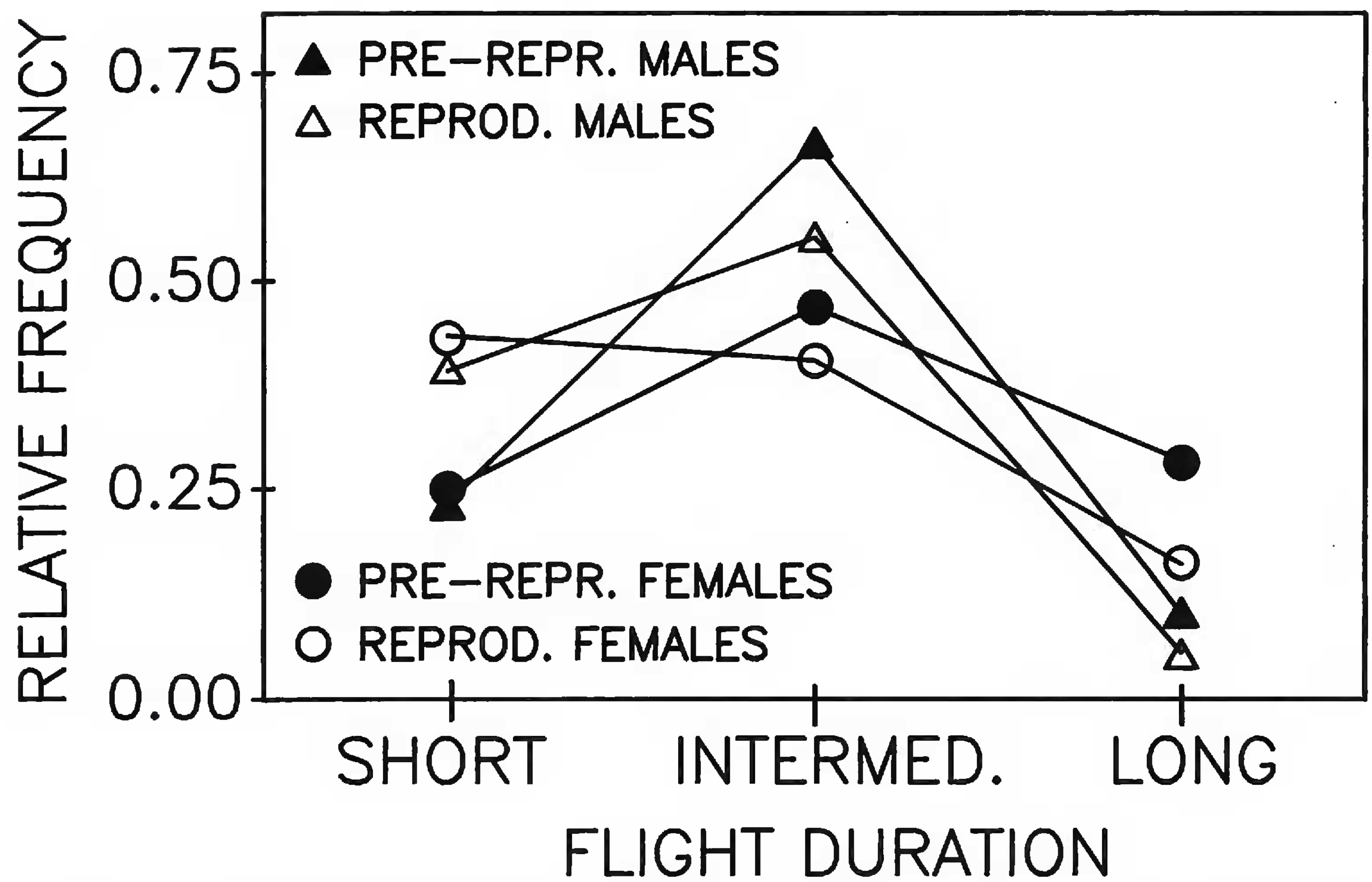

Figure 1. Observed (symbols) and fitted (lines) proportion of pear psylla for which the longest flight was short-duration (< 5 min), intermediate-duration (5–15 min), or long-duration (> 15 min). Lines show predictions from multiway categorical analysis: sex—χ^2 = 6.81, P = 0.033; reproductive status—χ^2 = 5.46, P = 0.065; likelihood ratio (= interaction): P = 0.996. For first flight (frequencies very similar to those shown for longest flight): sex—χ^2 = 7.1, P = 0.029; reproductive status—χ^2 = 6.4, P = 0.04; likelihood ratio (= interaction): P = 0.994. For average flight (data not shown), P-values both > 0.25.

We also classified flight durations (longest, first, mean) into one of three categories: short flight (< 5 min); intermediate flight (5–15 min); long flight (> 15 min). These data were analyzed as a 2 × 2 × 3 (sex × reproductive status × flight category) multiway categorical table using PROC CATMOD (SAS Institute 1987).

Product-moment correlation was used to determine whether there was any relationship between tibia length or the four wing measurements and the three estimates of flight duration (longest, mean, first). Analyses were done separately for each sex × collection date combination using the PROC CORR package of SAS (SAS Institute 1987).

Results

For longest flight and first flight, proportion of psylla falling in the short-, intermediate-, or long-duration flight categories varied with both sex and reproductive status (Fig. 1; results shown only for longest flight, as results for first flight were virtually identical). For both sexes, probability of intermediate- or long-duration flight was larger for pre-reproductive psylla than for reproductive psylla, whereas the converse was true for short-duration flights; i.e., for the latter, about 40% of reproductive psylla exhibited short-duration flight, whereas only about 25% of pre-reproductive psylla exhibited flights of this duration (Fig. 1). The

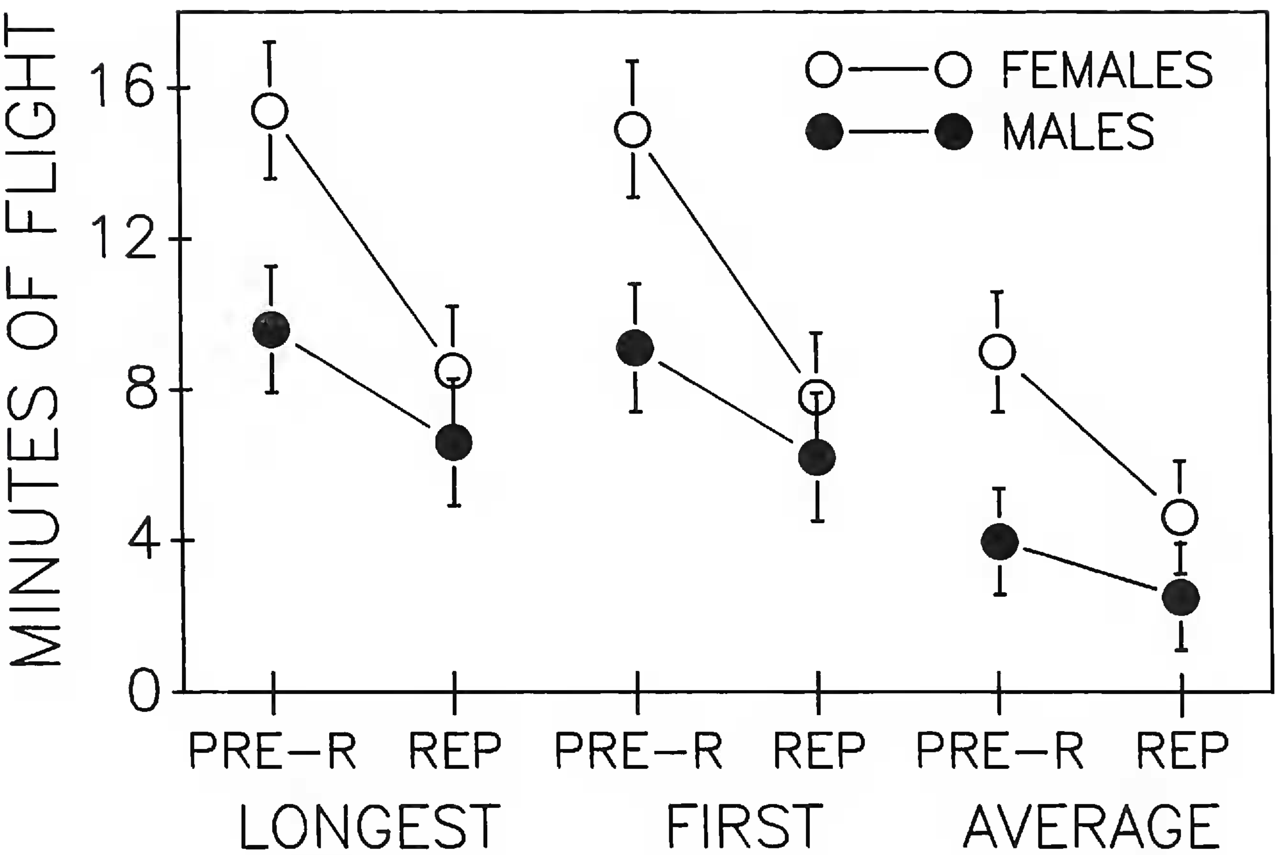

Figure 2. Mean (± standard error) flight durations (longest, first, average) for pre-reproductive (PRE-R) and reproductive (REP) pear psylla. Results of ANOVA (all effects df = 1,142); longest: sex—$F = 4.8$, $P = 0.029$; reproductive status—$F = 8.1$, $P = 0.005$; interaction—$P = 0.27$; first flight: sex—$F = 4.6$, $P = 0.034$; reproductive status—$F = 8.7$, $P = 0.004$; interaction—$P = 0.23$; average: sex—$F = 5.8$, $P = 0.017$; reproductive status—$F = 4.0$, $P = 0.049$; interaction—$P = 0.31$.

greatest difference between the sexes was in frequency of intermediate- and long-duration flights. Females exhibited a higher frequency of long-duration flights than did males, whereas males flew primarily intermediate-duration flights. Results are not shown for average flight duration, as reproductive status and sex effects were not significant (see Fig. 1 caption).

Mean flight durations varied with sex and reproductive status for all three estimates of flight duration (Fig. 2). For all measures, females exhibited larger mean durations than did males, and pre-reproductive psylla flew longer than did reproductive psylla (although $P = 0.049$ for reproductive status [average flight duration]; see Fig. 2 caption). There is a suggestion of a sex × reproductive status interaction for all three response variables (Fig. 2); however, in no case was the interaction significant (Fig. 2 caption).

For psylla that completed 5 flights, there was a significant decay in mean flight duration between the first flight and subsequent flights (Fig. 3). There was also a significant flight number × reproductive status interaction (Fig. 3 caption); the interaction was apparently due to large differences in flight durations between reproductive and pre-reproductive psylla for the first flight, but not for subsequent flights (univariate ANOVA for the first flight: reproductive status—$F = 7.8$; df = 1,133; $P = 0.006$; similar analyses for flights 2–5 were non-significant).

Males were significantly smaller than females (Table 1). However, within each sex × reproductive status category, correlations between the body size measurements and the three measures of flight duration (longest, mean, first) were non-significant.

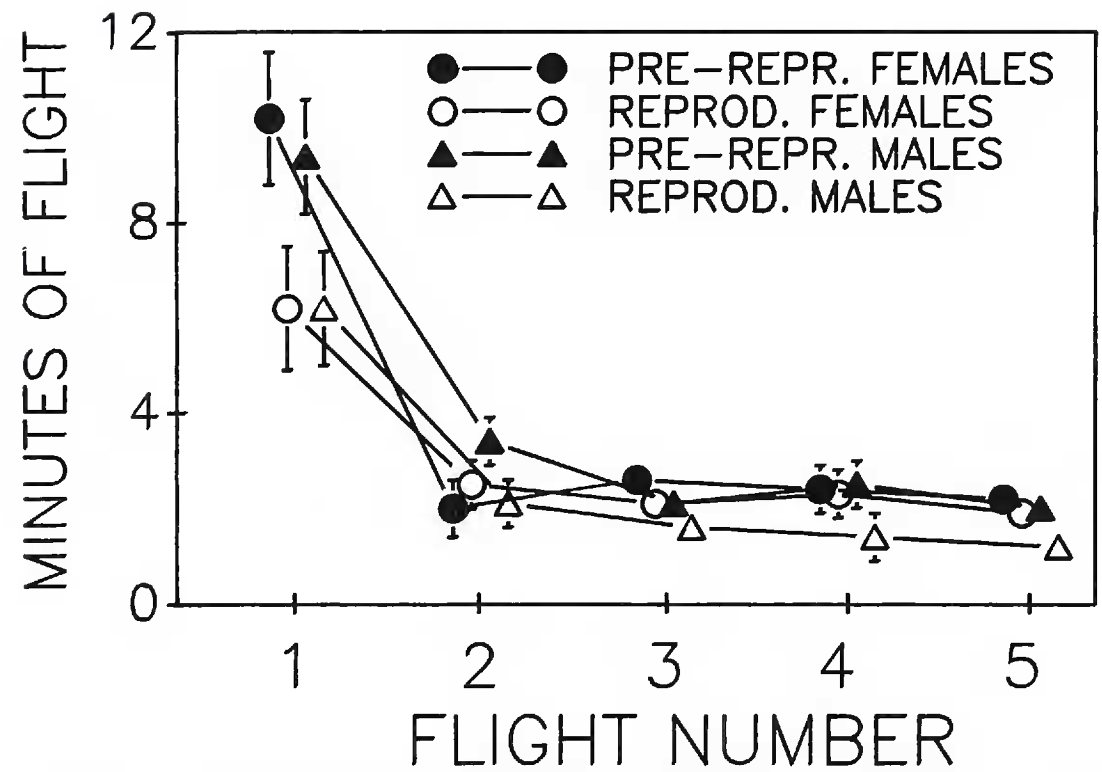

Figure 3. Mean (± standard error) flight durations of consecutive flights for pear psylla that completed 5 flights. Results of repeated measures ANOVA (within-subjects statistics from Wilks' lambda): flight number—$F = 28.3$, df $= 4{,}130$, $P < 0.0001$; flight number × reproductive status—$F = 2.5$, df $= 4{,}130$, $P = 0.04$; flight number × sex—$F = 1.5$, df $= 4{,}130$, $P = 0.21$; flight number × reproductive status × sex—$F = 2.0$, df $= 4{,}130$, $P = 0.10$; reproductive status—$F = 5.7$, df $= 1{,}133$, $P = 0.018$; sex—$F \ll 1.0$; reproductive status × sex—$F \ll 1.0$.

Discussion

Studies have suggested or shown for other insect species that females are more dispersive than males (Adesiyun & Southwood 1979, Reader & Southwood 1984, Stewart & Gaylor 1991) or that females exhibit longer flight durations than males in laboratory flight experiments (Dingle 1966, Davis 1986). In this study, female winterform pear psylla exhibited larger mean flight durations (Fig. 2) and a higher frequency of long (> 15 min) flights than did males (Fig. 1). Also, of the 146 insects tested, three flew continuously for 1+ h before being interrupted; all three were females (longest male flight was 46 min). As females are larger than males (Table 1), it is tempting to hypothesize that body size affected flight durations, as shown for other species (Dingle et al. 1980, Davis 1986, Saks et al. 1988, Roff 1991); however, we were unable to demonstrate a relationship between body size and flight duration within any of the 4 sample groups.

Fall-collected and spring-collected pear psylla did not differ substantially in flight duration, despite differences between the collections in ovarian development of psylla (DRH, unpublished data). Long-duration flights in many insects occur before significant ovarian development (Johnson 1969), so the results of the earlier study were unanticipated; but, see the discussion in Sappington & Showers (1992). In this study, there were significant differences in flight activities between the two collection dates, as psylla collected in late-March had reduced flight durations relative to psylla collected in January. One difference between this study and a previous study (DRH, unpublished data) is that the spring sample taken here occurred well after egg-laying had commenced in the field, whereas the spring sample in the other study occurred before egg-laying (March 1). This result suggests

Table 1. Mean (± standard error) body size measures (mm) of male and female winterform pear psylla collected in January (pre-reproductive) and late March (reproductive), 1993.

	Pre-reproductive		Reproductive	
Measure[a,b]	Females	Males	Females	Males
Tibia	0.56 (0.004)	0.54 (0.004)	0.55 (0.004)	0.54 (0.004)
LRC	0.65 (0.006)	0.56 (0.006)	0.63 (0.006)	0.57 (0.006)
LCM	0.55 (0.006)	0.51 (0.006)	0.55 (0.006)	0.50 (0.006)
Length	1.87 (0.014)	1.66 (0.012)	1.86 (0.012)	1.66 (0.012)
Width	1.07 (0.008)	0.97 (0.008)	1.06 (0.008)	0.97 (0.008)

[a] Final four measures are wing measures (see Materials and Methods).

[b] MANOVA (F-statistics from Wilks' lambda): sex—$F = 60.1$, df = 5,130, $P < 0.0001$; reproductive status—$F = 0.5$, df = 5,130, $P = 0.79$; sex × reproductive status—$F = 2.3$, df = 5,130, $P = 0.048$. Univariate tests: all five measurements differed between males and females ($P < 0.0001$, df = 1,134); for LRC, the sex × reproductive status interaction is significant ($P = 0.012$, df = 1,134); reproductive status main effects were non-significant for all five measures ($P > 0.25$).

that long duration flights decreased in frequency as psylla became fully engaged in egg-laying.

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